Synopsis and Discussion of the Association
of Ctenidia and Labial Palps in the Bivalved Mollusca

BY

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(5 Text figures)

As well described by Yonge (1939), classical understanding of evolution within the bivalved Mollusca has the Nuculidae as ancestral types of all other members of the class. In his functional interpretation of protobranchiate structure, Yonge was apparently led to conclude that the anatomy of Recent Nuculidae is thus a true reflection of primitive conditions. Among these conditions was the presence of extensible palp appendages or proboscides with which the organisms fed directly upon deposits in the substratum. Correspondingly there was believed to be a lack of association of ctenidia and labial palps, an association typifying lamellibranchiate groups, all of which rely upon the ctenidia as food collecting and primary food sorting organs. As in the Nuculidae, the palp lamellae of other bivalves sort the gathered particles prior to ingestion.

The classical view of evolution within the Bivalvia may be summarized in several ways; namely, taxonomically (Nuculidae → higher Bivalvia), anatomically (lack of gill-palp association → gill-palp association), and functionally (proboscidial deposit feeding → suspension feeding).

With the classical view well in mind it is significant that recent work (Stasek, 1961) demonstrated an anatomical feeding association of ctenidia and labial palps in the Nuculidae. While it is true that the ciliated palp proboscides convey large quantities of potential food into the mantle cavity, the relative functional importance of the various methods of feeding in the family remains speculative; particles trapped by the ctenidia may be almost wholly ingested, whereas masses gathered by the proboscides seem to be more rigorously subject to sorting and rejection. Although lacunae exist in our knowledge, the Nuculidae can no longer be thought to exemplify the now hypothetical primitive condition in which the ctenidia lack close relationship with the labial palps.

The discovery that a well defined association of gill and palp is present in the Nuculidae led me to study the relationship of these organs throughout the Bivalvia. The present paper describes only the broadest anatomical features of the relationship as determined from 55 families of the class. Of these, conditions in six were not personally observed but were deduced from illustrations in carefully chosen papers in the literature, which is generally unreliable in this respect.

Synopsis of Observations

To date, specimens of 193 species in 127 genera have been studied. Observed associations of ctenidium and palp may be segregated into three major anatomical categories:

Category **I** is one in which the ventral tips of at least the first few or, usually, of many anterior filaments of the inner demibranch are inserted *unfused* into a distal oral groove (a designation originated by Kellogg, 1915). Exemplary types are *Acila castrensis* (Hinds, 1843) (Nuculidae, Fig. 1) and *Anodonta californiensis* Lea, 1852 (Unionidae, Fig. 1). Category I characterizes the following groups: Nuculacea, Mytilacea, Unionacea, Astartidae, and possibly the Trigoniacea (Pelseneer, 1891).

Category **II** is one in which the ventral tips of the anteriormost filaments of the inner demibranch are inserted into *and fused to* a distal oral groove. An exemplary type is *Clinocardium nuttalli* (Conrad, 1837) (Cardiidae, Fig. 1). Category II characterizes the following groups: Carditacea, Isocardiacea, Cyprinacea, Chamacea, Cardiacea, Veneracea (with certain exceptions being placed in Category III), Mactracea (in part), Semelidae, Gastrochaenacea, *Xylophaga* (?) and Lyonsiidae.

Category **III** is one in which the ventral tips of the anterior filaments of the inner demibranch are not inserted into a distal oral groove, although the antero-ventral margin of the inner demibranch may be fused to the inner palp lamella as in *Mactra dolabrata* Reeve, 1854 (*ex* Deshayes MS) and *Macoma nasuta* (Conrad, 1837). Exemplary types are *Kellia laperousii* (Deshayes, 1839)
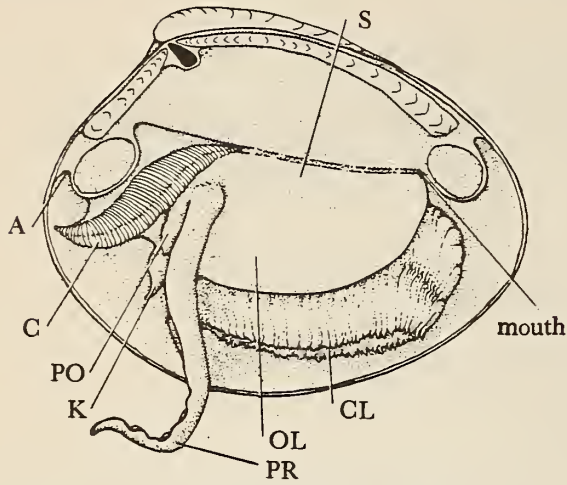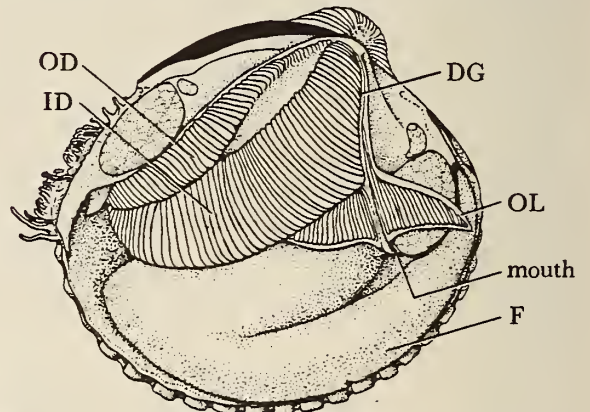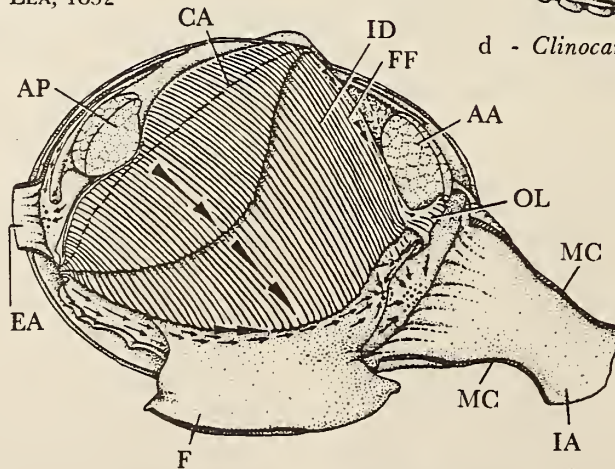
a - *Acila castrensis* (HINDS, 1843)
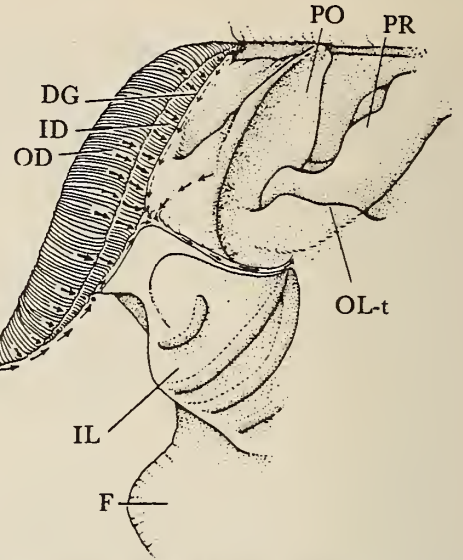
b - *Acila castrensis*: Association of ctenidium and palp
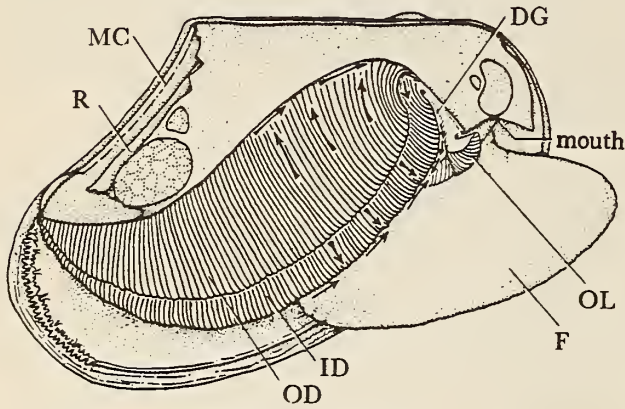
c - *Anodonta californiensis* LEA, 1852

d - *Clinocardium nuttallii* (CONRAD, 1837)

e - *Kellia laperousii* (DESHAYES, 1839)

Figure 1: Major associations of ctenidium and labial palp exemplified by *Acila* and *Anodonta* (Category I), *Clinocardium* (Category II), and *Kellia* (Category III).

up to 1 cm long (Erycinacea, Fig. 1) and *Isognomon costellatus* (Conrad, 1837) (Pteriacea, Fig. 2). Category III characterizes the following groups: Arcacea, Pteriacea, Pectinacea, Anomiacea, and Ostreacea, as well as Crassatellidae, Sphaeriacea, Cyamacea, Lucinacea, Erycinacea, some Veneridae (*Transenella, Psephidia, Gemma*), Cooperellidae, Mactracea (in part), Tellinacea (except *Semele*), Solenacea, Saxicavacea, Myacea, Adesmacea (*Xylophaga* possibly excepted), Pandoracea (except Lyonsiidae), and Clavagellacea (in Purchon, 1956, p. 46). The Septibranchia seem also to be in this category.

Extensive subdivision and some intergradation of these categories exist, but these will not be discussed here.

Discussion

Of the three structural levels observed in the association of ctenidia and labial palps Category I is interpreted as the most primitive, for it occurs in the widely divergent Protobranchia (Nuculidae and Nuculanidae) and in some filibranch and eulamellibranch representatives. Among the latter are the Astartidae, generally thought to be relatively conservative descendants of the group from

That there are thought to be at least two major lines of evolution in the Bivalvia was discussed in a previous summary of the literature (Stasek, 1961, p. 535). One line stemmed from the Late Cambrian ctenodonts and led to the Nuculidae, Nuculanidae, Malletiidae, and, possibly, to the Septibranchia (Purchon, 1963). A separate line arose from the Ordovician actinodont group, which, after early adaptive radiation, apparently gave rise to all lamellibranchiate bivalves. There are no known intermediate fossil forms demonstrating the evolution of the actinodonts from the ctenodonts, and comparative anatomical studies of their respective descendants often have demonstrated what are taken to be great differences, for example between the ctenidia (Pelseneer, 1911), the digestive systems (Owen, 1959; Purchon, 1963), and the dentition (Cox, 1959). However, the similarities between the association of gill and palp in many of their descendants, together with the widespread presence of eu-latero-frontal cilia on the ctenidial filaments (Atkins, 1938), is evidence establishing some close affinity between these otherwise little related and remote fossil groups.

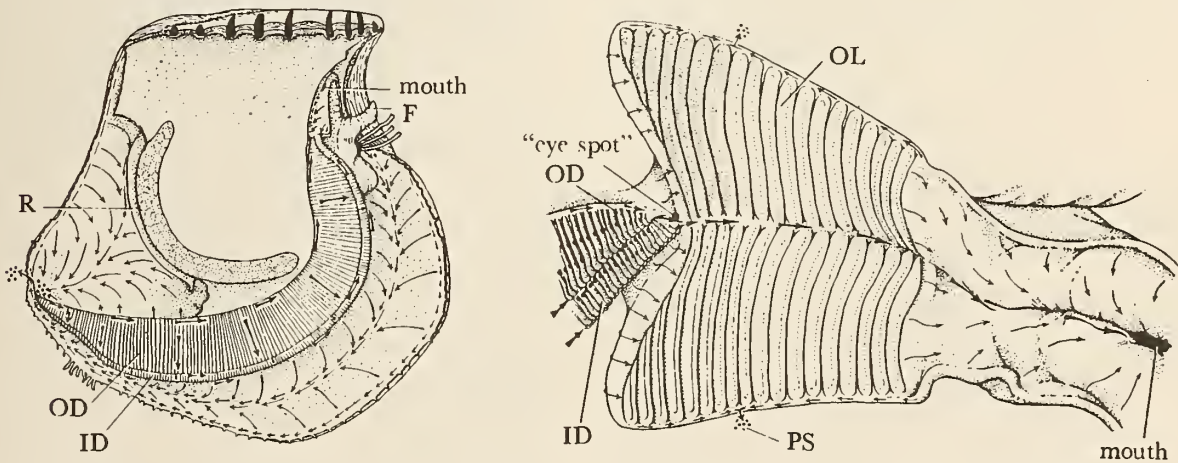Collation of stomach types, as described by Purchon

Figure 2: *Isognomon costellatus*. Mantle cavity and detail of association of ctenidium and labial palp (Category III).

which the remainder of the Heterodonta arose (Nicol, 1955). That the most primitive existing condition is one in which the filter-feeding mechanism is highly developed may be emphasized. As evidenced by the apparently minor rôle the association plays in gathering food in the Nuculidae, a rôle one can hardly envisage as having evolved if the palp proboscides were pre-existing, efficient food collectors, the presence of such similar associations in diverse and otherwise primitive families indicates that one is not here dealing with an instance of convergent evolution.

(see Purchon, 1963) and the association of ctenidium and palp indicates that while near the bases of the major evolutionary lines the association of gill and palp has been more conservative than the structure of the stomach, the reverse is true at other levels. For example, in astartids and carditids, both with stomachs of type 4, adults of the former comprise a subgroup in Category I while adults of the Carditidae are in Category II.

Category II seems to have come about by fusion of the ctenidial filaments to the distal oral groove. All known

species in this category are eulamellibranchiate. If one assumes that an association of this kind arose prior to the dichotomy leading to the development of a stomach of Type 5 from one of Type 4 (see Purchon, 1963), the appearance of an association of Category II in groups with either type of stomach is not surprising. All groups in this category are concluded to be diversely descended from some large, common-ancestral group and to be more primitive with respect to the association of ctenidium and palp than their relatives in Category III.

Groups in which the adults are characterized by an association of Category III appear to have arisen either from groups in Category II by prolongation of the period of growth of the anterior-most filaments of the inner demibranch (e. g. *Kellia*) or from groups in Category I through extreme inhibition of the development of the anterior regions of the body (e. g. *Chlamys*, see Stasek,

Figure 4: *Glycymeris subobsoleta*. Mantle cavity and detail of association of ctenidium and labial palp.
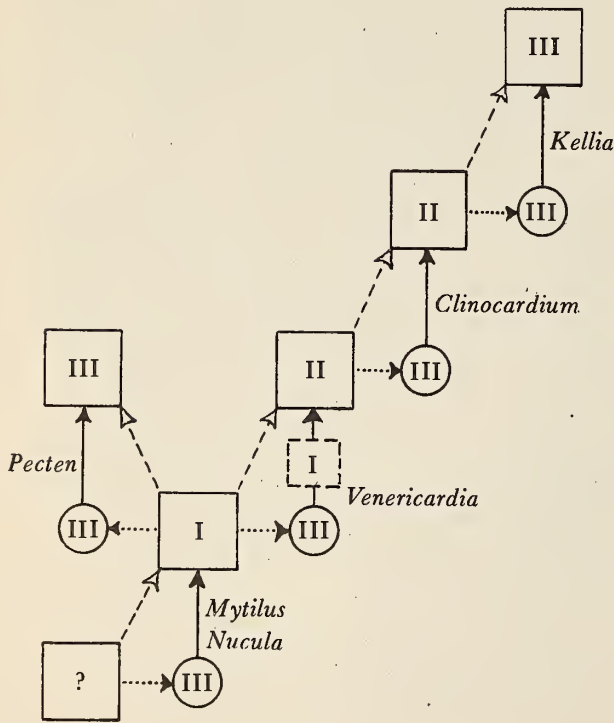

Figure 3: Phylogenetic and ontogenctic progression (dashed and solid arrows respectively) of the associations of the ctenidium and labial palp. Condition in adults indicated by large squares; probable condition in post-larval stages by circles; transient condition by small square. Dotted arrows suggest that evolutionary changes occur by modification of ontogenics through successive generations. No actual phylogenetic relationship of exemplary genera is meant to be implied.
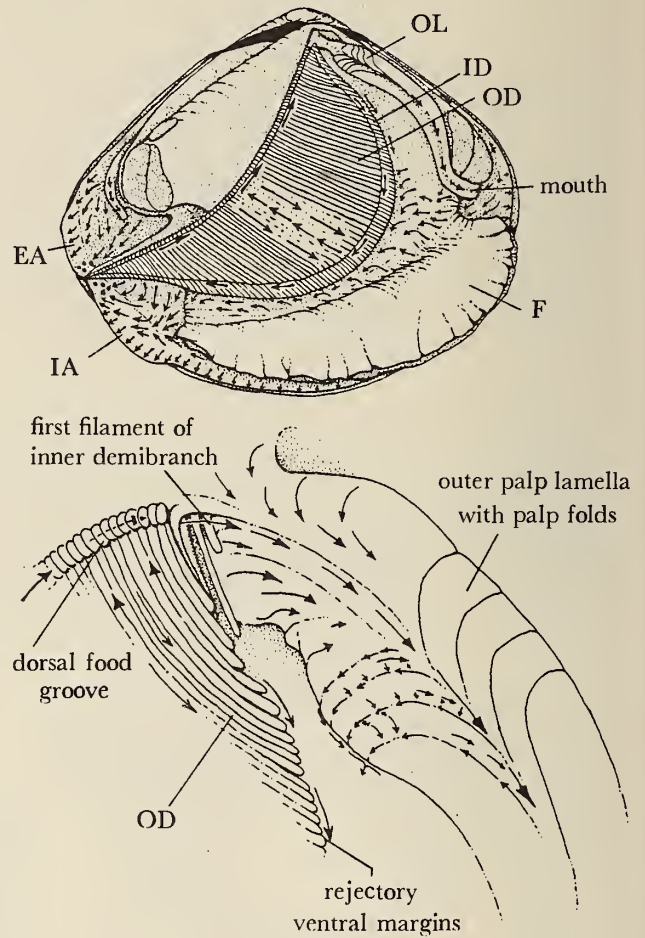
Explantion of abbreviations used for all text figures:

A - anus   AA - anterior adductor
AP - posterior adductor   C - ctenidium
CA - ctenidial axis   CL - cleft in foot
DG - distal oral groove   EA - exhalant aperture
F - foot   FF - first ctenidial filament
IA - inhalant aperture   ID - inner demibranch
IL - inner palp lamella   K - keel of foot
Ma - mantle   MC - mantle cut
OD - outer demibranch   OL - outer palp lamella
OL-t - outer palp lamella turned back
PO - palp pouch   PR - palp proboscis
PS - pseudofeces   R - rectum
S - suspensory membrane of palp

1963). Taxa in Category III are not necessarily related, there having been several convergent evolutionary trends. Probable phylogenetic progression of the relation of gill and palp is illustrated by dashed arrows in figure 3.

While Category III appears to be the most modified in terms of phylogeny, it seems to be the association first appearing in the ontogeny of every species for which suitable information exists. Kinds of ontogenetic progression are shown by unbroken arrows in figure 3. Wherever an association of Category III is encountered in the adult, evolutionary trends towards juvenilization are concluded to be the cause. Juvenilization may occur either through relatively unmodified prolongation of growth of the early post-larval arrangement, affecting many other organs as well (e. g. in the Erycinacea and the Lucinidae, see STASEK, 1963), or through extreme relative retardation of the formation of a distal oral groove (e. g. in the Pteriacea and Pectinacea). Relative retardation, which involves the whole of the anterior regions of the body and mantle/shell (STASEK, 1963), may be lesser, as in the Mytilacea (Category I), or greater, as in *Isognomon,* and generally results in a derived condition in which both inner and outer demibranchs are embraced by the palp. Also, the ctenidial axis empties very near the juncture of the two palp lamellae (Fig. 2). The view that this is a derived condition is contrary to general belief. For example, YONGE (1939, p. 134) considered it to be an intermediate stage in the evolution of the Eulamellibranchia. Notwithstanding the very few exceptions, such as large *Mya arenaria,* the normal and primitive condition in isomyarian Bivalvia is one in which only the inner demibranch is embraced by the palp lamellae, the axis of the ctenidium passing obliquely to, and not nearly parallel with the antero-posterior axis of the body (compare figs. 1 and 2). The scheme envisaged by previous investigators may have been influenced by the prevalent concepts of PELSENEER (1911, p. 123) who mistakenly considered the Mytilidae to have given rise to all the Eulamellibranchia.

The situation seen in extreme anisomyarian families such as the Isognomonidae (Fig. 2) also characterizes the Arcacea (Fig. 4). The anatomical arrangement in the former is clearly allied with relative inhibition of growth of the anterior regions, a process leading to a heteromyarian or monomyarian condition. The very similar association of ctenidium and palp in the nearly isomyarian Arcacea, for example *Glycymeris,* is surprising, especially since neontologists usually regard that genus as an "unmodified equilateral isomyarian" (YONGE, 1962, p. 451). The probable truth of the matter emerges when the fossil record is taken into account. In a revealing paper, NICOL (1950) concluded that the Glycymeridae were derived from the Cucullaeidae (probably *Idonearca*) during Late Jurassic times. The Cucullaeidae are inequilateral and

somewhat heteromyarian. That family and the Arcidae seem to have arisen as separate stocks from the complex arcacean genus *Parallelodon* (ARKELL, 1930), the Cucullaeidae sometimes being regarded as members of the Parallelodontidae (REINHART, 1935, p. 8; DECHASEAUX, 1952, p. 270). The Parallelodontidae were probably descendants of the Ordovician actinodonts, a group showing remarkable variation in form (*cf.* DOUVILLÉ, 1912). Some, such as *Actinodonta acuta,* were isomyarian while others, such as *A. obliqua* and *Cyrtodonta declivis,* were heteromyarians. It was in the cyrtodont type that ARKELL (1930) and NEWELL (1954) perceived the origin of the Arcacea. If this is true, Recent Arcacea had heteromyarian ancestors in which both demibranchs were probably embraced by the palp lamellae. Through time, there seems to have been an equalization of growth rates of anterior and posterior regions of the body and mantle/shell resulting in the Glycymeridae, a secondarily derived isomyarian and equilateral type, but one in which the probably ancient association of ctenidium and palp has been retained. This process has actually carried *Glycymeris* beyond an isomyarian state to one in which the anterior adductor is somewhat larger than the posterior (ABBOTT, 1954, p. 348). Conditions in the Arcacea thus provide an example in which adaptations of the ancestors partially restricted the further evolution of their phylogenetic offspring.

Conclusion

Associations of ctenidium and palp in existing species may be correlated with time of appearance of higher taxa in the fossil record to result in a scheme illustrating the probable temporal interconnections of the three major categories (Fig. 5). Correlation with other organ systems has allowed subdivision within groups with similar ctenidium-palp associations. Basic assumptions have been that categories I and II each arose only once and that any of the taxa named have, since their appearance, retained the general original character of the association. Minor alterations have occurred but have not been discussed. A third assumption has been that all extinct and as yet unstudied existing species have been or will be characterized by one of the three major categories described. Comparative use of further characters would aid in separating groups parallel or convergent in the few features used and in bringing together groups believed on other grounds to be closely related (i. e. the Lucinidae and Diplodontidae, the Lyonsiidae and Pandoridae, etc.). Thus, too few anatomical systems have been employed in figure 5 to justify a claim that all levels of the "tree" validly depict close taxonomic relationship. I concur with RIDEWOOD (1903) that in Recent species correlation of several organ systems will provide a more reasonable understanding than now exists of the past history and

Isocardiacea, Cyprinacea, Chamacea, Cardiacea, Veneracea, Mactracea (part)

Diplodontidae, Corbiculidae, Myacea, Mactracea (part)
Tellinidae, Psammobiidae, Pholadidae, Solenacea

Lucinidae, Thyasiridae, Sphaeriidae, Cyamiacea, Erycin-
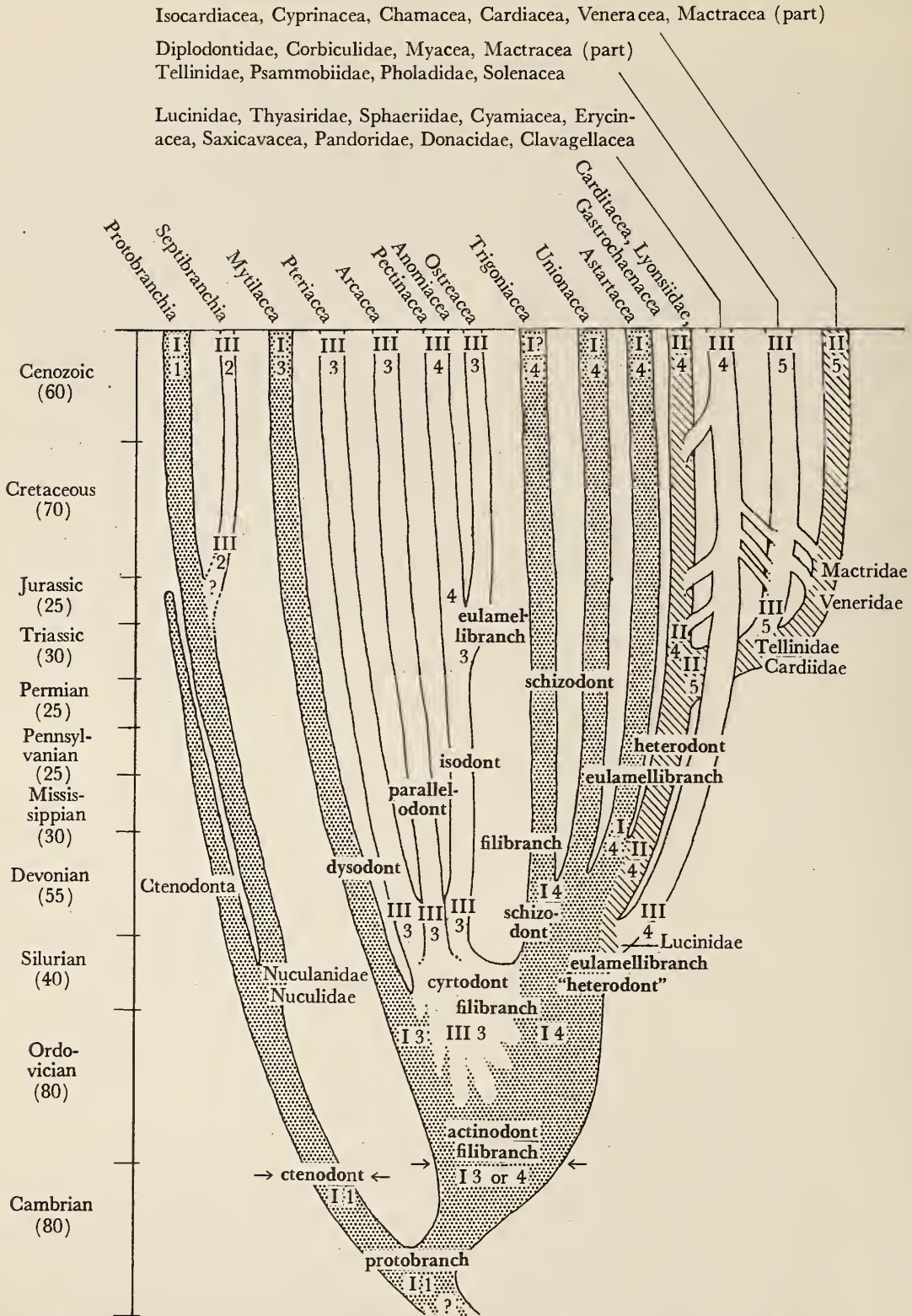acea, Saxicavacea, Pandoridae, Donacidae, Clavagellacea

Figure 5: Tentative phylogenetic tree of the Bivalvia as obtained through correlation of the fossil record (data mainly from DECHASEAUX, 1952), the association of ctenidium and palp (Roman numerals), stomach type (Arabic numerals), dentition, and gill type. Possible interconnections of the three major associations of ctenidium and palp are indicated by stippling (Category I), cross-hatching (Category II), and blank spaces (Category III). Arrows suggest first appearance of major lines in fossil record. Duration of geological divisions is in millions of years (NICOL et al., 1959, p. 353).

interrelations of the Bivalvia. There is no need to believe that changes in one system will have been simultaneous with those in other systems; the persisting search for a single most "objective" taxobasis has been, is, and probably will continue to be futile. MARCH (1912), PURCHON (1958), and Cox (1960) have outlined and discussed previous attempts at phylogenetic classification in the Bivalvia.

ACKNOWLEDGMENTS

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